The potential for top-down control on tropical tunas based on size structure of predator-prey interactions

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Abstract

The ecological consequences of widespread fisheries-induced reductions of large pelagic predators are not fully understood. Tropical tunas are considered a main component of apex predator guilds that include sharks and billfishes, and thus may seem unsusceptible to secondary effects of fishing top predators. However, intra-guild predation can occur because of size-structured interactions. We compiled existing data of apex predator diets to evaluate whether skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas might be vulnerable to top-down control by large pelagic predators in the eastern tropical Pacific Ocean. We identified potentially important predators on tunas by the frequency, quantity, and size/age of tunas in their diets and considered the degree that predated tunas could have potentially contributed to the reproductive output of the population. Our results indicate that the proportion of predator diets consisting of skipjack and yellowfin tuna was high for sharks and billfishes. These predators also consumed a wide size range of tunas, including sub-adults are capable of making a notable contribution to the reproductive output of tuna populations. Our study suggests that, in the eastern tropical Pacific Ocean, tropical tunas act as mesopredators more so than apex predators. Sharks and billfishes have the potential to play an important role in regulating these tuna populations. This study sets the stage for future efforts to ascertain whether diminished levels of large predators have enhanced the production of tuna stocks, and if the trophic interactions of skipjack and yellowfin tunas should be explicitly accounted for when assessing their population dynamics.

Keywords: Predator release, top-down control, apex predators, size structure, ecosystem-based management, mesopredator, reproductive value

Introduction

There is growing evidence in a diversity of marine ecosystems that apex predators can regulate the productivity and abundances of their prey populations (see Baum & Worm 2009, Ritchie & Johnson 2009). There is also widespread recognition that fishing has altered the structure of marine food webs through the selective removal of large-bodied predators (Estes et al. 1998, Jackson et al. 2001, Worm & Myers 2003, Daan et al. 2005, Frank et al. 2005, Ward & Myers 2005, Daskalov et al. 2007). Fishing can therefore be viewed as an important structuring agent in marine food webs, promoting productivity of mesopredators (i.e. species that occupy a trophic positions immediately below apex predators) that thrive following the depletion of their larger-bodied predators (e.g. Worm & Myers 2003, Frank et al. 2005, Polovina et al. 2009). A better understanding of the effects of predator removals on species dynamics is key to implementing ecosystem-based fisheries management. Identifying the magnitude and extent of these effects in many marine ecosystems remains a challenge owing to a paucity of historical data and monitoring surveys, and the confounding effects of dynamic ocean conditions (Essington 2010).

Top predators in high seas pelagic food webs have been subjected to large-scale fisheries for the past half-century. In the tropical Pacific Ocean, the apex predator guild (i.e. predators that occupy the top trophic positions and consume similar prey resources) is composed of large tunas, sharks, and billfishes (Seki & Polovina 2001, Kitchell et al.

77 2002). Highly-valued skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus*
78 *albacares*) populations are the primary targets of purse seine and longline (yellowfin tuna
79 only) fisheries. These populations are currently considered to be healthy and productive,
80 and are above (skipjack tuna; Maunder and Harley 2005) or near (yellowfin tuna;
81 Maunder and Aires-da-Silva 2009) management targets that maximize fishery catch.
82 However, shark and some billfish populations have declined substantially over the last
83 several decades as a result of fisheries exploitation and incidental captures (Baum et al.
84 2003, Ward & Myers 2005, Sibert et al. 2006, Minami et al. 2007). The ecological
85 consequences of reduced abundances of these large predators in the Pacific Ocean are
86 becoming increasingly apparent. Recent studies indicate a shift in the north Pacific
87 subtropical gyre food web, whereby smaller, fast-growing, short-lived mid-trophic level
88 mesopredators have become more abundant in response to apex predator reductions
89 (Ward & Myers 2005, Polovina et al. 2009).
90 Tropical tunas, particularly yellowfin tuna, are often considered members of the
91 apex predator guild and thus seem unlikely to be strongly regulated by predation.
92 However, tunas are vulnerable to cannibalism and intra-guild predation from species that
93 are also impacted by commercial fishing activities. For example, large-bodied marlins
94 commonly consume skipjack and yellowfin tunas (Brock 1984), pelagic sharks are
95 widely viewed as opportunistic top predators (Cortes 1999), and skipjack and yellowfin
96 tunas consume juvenile conspecifics with some regularity (Alverson 1963, King &
97 Ikehara 1956). Thus, it is possible that tropical tunas actually fill the role of
98 mesopredators during much of their life history. If this hypothesis is true, their
99 productivity may be enhanced by the depletion of larger-bodied species. This is a

100 potentially important consideration for high-seas fisheries management. Strategies to
101 restore depleted shark and billfish populations (Kerstetter & Graves 2006, Kaplan et al.
102 2007, Gallucci et al. 2006, Pine et al. 2008, Watson et al. 2009) could diminish the
103 production capacity of tuna species (Kitchell *et al.* 1999, Cox et al. 2002; Olson and
104 Watters 2003) and thereby introduce conflicts and trade-off issues between the economic
105 objectives of tuna fisheries and the conservation and economic objectives for billfishes
106 and sharks.

107 Here, we evaluate whether large-bodied apex predators might be capable of
108 regulating skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tuna
109 populations. Strong top-down interactions can be identified by population modeling and
110 statistical analysis of retrospective data (Worm & Myers 2003, Frank et al. 2005) or by
111 bioenergetics principles (Williams et al. 2004). However, the information needed to
112 support these approaches is not available for most pelagic fishes inhabiting open-ocean
113 ecosystems. Instead, we adopt an approach used to gauge the importance of
114 anthropogenic-induced mortality on large pelagic species: one that considers the life
115 history stages impacted and the reproductive potential of the fish at those stages (Gallucci
116 et al. 2006, Maunder & Harley 2005, Wallace et al. 2008, 2010). Estimates of
117 reproductive potential have been used to identify the ages/sizes in the population that are
118 most valuable for future population growth, and therefore should be avoided by fisheries.
119 (Caddy & Seijo 2002, Maunder & Harley 2005). We use similar criteria to distinguish
120 between a species' ontogenetic changes in predation risk versus its overall vulnerability
121 to predators, revealing the predators that are most likely to regulate tuna productivity. We
122 presume that predators that consume substantial numbers of the large juvenile or sub-

adult tunas that have notable reproductive potential can have a potentially important impact on the intrinsic rates of growth, on biomass and ultimately, on sustainable catch levels of tuna populations. Thus, predators that prey on tunas that have high reproductive value are the species most likely to regulate tuna productivity.

This study provides the most detailed and comprehensive evaluation of intra-guild predation on tropical tunas to date. Unique to this work is the development and use of an apex predator food habits database that includes summarized data on nearly 25 predator groups and primary data on 65 predator groups inhabiting the tropical Pacific Ocean. We compiled all known apex predator food habits data from published papers and reports, and digitized primary data records from sampling ventures that span more than five decades. The spatial extent of the summarized data includes much of the range of the tropical tunas in the Pacific Ocean, while the primary data are restricted to a large portion of the eastern tropical Pacific Ocean. To the primary data we applied statistical models to develop robust estimates of predation frequency and intensity and also to explore important environmental and biological covariates therein. We then compared the size structure of skipjack and yellowfin tunas consumed by top predators to estimate reproductive potential-at-size lost to predation.

Materials and Method

Food habits data

We compiled data on the food habits of large- and medium-bodied fishes commonly considered apex predators, using three methods. First, we compiled primary data from three food habits studies of the Inter-American Tropical Tuna Commission

146 (IATTC) into a common database format. Second, we digitized primary data reported in
147 archived data sheets belonging to the IATTC (see Supporting Information Appendix S1
148 for details). Third, we compiled published food habits data summarized in either reports
149 or peer-reviewed publications (See Supporting Information Table S1 and Appendix S2).
150 The resulting data set is a compilation of both primary and summarized data that lend
151 themselves to different types of analyses. The primary data contained detailed
152 information on individual samples and were used for formal statistical analyses. The
153 summarized data provided accounts of the feeding habits of various predators, which we
154 used to generate broad comparisons across predator taxon/taxa and to assess the
155 generality of the findings across regions of the tropical Pacific Ocean.

156 The primary data encompassed an area south of the Hawaiian Islands and a large
157 portion of the eastern Pacific Ocean (Fig. 1). These data were clustered among two
158 historical periods (1955-1960, 1969-1972) and two contemporary periods (1992-1994,
159 2003-2005). Primary data from the contemporary period were collected by observers
160 aboard purse-seine fishing vessels, and consisted of approximately 65 predators, whereas
161 data from the historical period contained information on the feeding habits of only
162 yellowfin tuna. The primary contemporary data provided information on individual
163 predators, including prey composition, date/time of capture, capture method/gear, the
164 precise spatial coordinates and sea surface temperature (SST) at the capture locations,
165 and predator and prey sizes. The historical data were yellowfin tuna sampled at canneries,
166 and therefore did not contain the same degree of detail regarding sampling dates,
167 locations, and SSTs (details below).

168 In total, the summarized data included nearly 24 predator taxon/taxa from 37
169 published reports or journal articles. At a minimum, these data sources contained
170 information on the range of predator body sizes sampled and the proportional
171 contribution of prey species to predator diets. The spatial extent of the summarized data
172 spanned much of the geographical range of skipjack and yellowfin tunas in the Pacific
173 Ocean and the temporal coverage ranged from the mid-20th century to the present. We
174 note that sharks and billfishes sampled for diet composition were not only (nor mostly)
175 large adults, but also included small individuals. For example, 18% of the shark
176 specimens were smaller than 90 cm total length, and 62% were smaller than 150 cm
177 (range 39-315 cm). This is consistent with the shark bycatch composition for the same
178 years (Román-Verdesoto et al. 2005).

179

180 Contribution of tunas to predator diets

181 We fit generalized linear mixed models (GLMMs) to the primary food habits
182 data to identify the predators that consume tunas more frequently and in relatively higher
183 quantities, while accounting for confounding physical and biological factors and potential
184 sampling biases. Pseudo-replication is a concern when the stomachs of several predators
185 are collected at the same sampling event (e.g. from the same purse-seine set). Because
186 these stomach samples are not independent, we modeled the relationship between
187 individual samples and sampling events as random effects (sampling event as grouping
188 variable, Gelman & Hill 2007).

189 Our analysis of primary data also needed to account for sampling biases
190 associated with changes in the methods of catching tunas and other predators over time

191 (via fishing vessels). The widespread use of human-made floating-object[1], i.e. fish
192 aggregating devices (FADs), in tuna purse-seine fisheries began after the 1969-1972
193 sampling period. Most purse-seine sets on FADs are made in the early morning when the
194 stomachs of most predators tend to be empty, and predators with empty stomachs were
195 excluded from the analysis to account for this sampling bias. Recently consumed tunas
196 were also excluded from the analysis to omit predation that likely occurred while the
197 animals were encircled in the purse seines. Lastly, for cases in which primary data
198 contained prey items that could be only identified to genus *Thunnus* sp., we assumed that
199 these prey were yellowfin tuna. This assumption was based on the observation that
200 yellowfin tuna was the most common species of *Thunnus* preyed upon, based on archived
201 predator food habits records for prey that were possible to identify (~95% of *Thunnus*
202 species consumed by predators were yellowfin tuna).
203 Because of the high number of zeros in the data (i.e. many stomachs that
204 contained no tunas), standard statistical probability distributions could not be used.
205 Instead we used a mixture model (also known as delta-normal or two-stage hurdle model;
206 e.g. Maunder and Punt, 2004, Jensen et al. 2005, Reum et al. 2011) wherein two separate
207 models were fit separately describing the frequency of occurrence and the mean mass (%)
208 conditional on a tuna being present. The two stages were then combined by taking the
209 product of the predicted values to generate an overall predicted diet proportion.

[1] Purse-seine sets are made in three different ways in the eastern tropical Pacific Ocean: in "dolphin sets" the net is deployed around the tuna-dolphin aggregation after a chase by speedboats; in "floating-object" sets, the net is deployed around or next to flotsam or fish-aggregating devices that attract tunas; in "unassociated sets", nets are set around free-swimming schools

In the first stage, we modeled the presence /absence data for skipjack and yellowfin tunas using a binomial probability density function and logit link function:

$$\text{logit}(y) = \log(y/(1- y)) = \beta x_{it} + \alpha_i + \varepsilon_{it} \qquad (1)$$

where y is the probability that a tuna was present in an individual predator's stomach, x_{it} is a vector of fixed effects, β is a vector of coefficients, α_i is a random effect (i.e. fishing event ID), and ε_{it} is the error term. The random effect is assumed to be distributed as $N(0,\sigma^2_\alpha)$

Second, for those stomach samples in which tunas were found, we estimated the proportional mass contribution of skipjack and yellowfin tunas to the total food mass in the stomach of each individual predator. Hence we refer to the response variable as the conditional percent mass contribution (u). For this second-stage analysis, we normalized the proportion estimates using the arcsine-square root transformation (Zar 1999) and modeled the response variable as a Gaussian (normal) probability density function with the identity link function:

$$u = \beta x_{it} + \alpha_i + \varepsilon_{it} \qquad (2)$$

This model is equivalent to a multiple regression model with a random effects term. In addition, we weighted the likelihood of each data point so that diet proportions of actively feeding fish were given more weight than diet proportions of fish with few prey in their stomachs. The weighting term is the ratio of predator stomach mass to fish mass.

232 To account for the confounding effects of spatial and temporal factors on
233 predators' feeding habits, we formulated a suite of candidate models that included all
234 combinations of one, two, or three sets of fixed effects (Table 1). The sets of potential
235 model covariates were the following: time period (data sets 1955-1960, 1969-1972, 1992-
236 1994, 2003-2005), season/quarter (winter, December-February; spring, March-May;
237 summer, June-August; autumn, September-November), set type/gear[1] (purse-seine
238 floating-object sets, dolphin sets, and unassociated sets; and pole-and-line gear), and
239 space (latitude, longitude, Area (1-4)); and predator (see Table 2 for levels). Latitude and
240 longitude were continuous variables, and prior to analysis they were standardized to have
241 means of zero and variances of 1 to simplify interpretation of the coefficients. The
242 remaining fixed effects were categorical.
243 Our modeling of primary food habits data took into account inconsistencies in
244 the historical food habits records. During the 1969-1972 sampling period, predators were
245 sampled from wells (i.e. partitions in the hold of the vessel into which the catch is
246 delivered) that contained multiple sets (typically 3-5 sets), each with known dates and
247 locations and each in proximity to one another (i.e. within < 1 degree by latitude and
248 longitude). Given that the exact set that yielded a sample could not be determined, we
249 averaged the estimates of latitude and longitude at the possible locations from which an
250 individual was captured to generate a single value of these physical parameters for each
251 predator. To further account for the confounding effects of space we included spatial area
252 as a model covariate. Four distinct areas (quadrants) were determined from the median
253 latitudinal and longitudinal coordinates of predator sampling location. We could not
254 include SST as an environmental variable. SST was routinely collected in the

255 contemporary sampling period, but not during the historical period, and we were unable
256 to reconstruct SST at many of the 1950s sampling locations. The data for predator
257 taxon/taxa that consumed tunas, but had low sample sizes (<20) were combined into
258 higher taxonomic groupings. One consequence of this modification is that the number of
259 predators considered in the GLMMs (and hence number of estimated parameters)
260 differed between the skipjack and yellowfin models (Tables 1 and 2). Predator taxon/taxa
261 were excluded from the analysis if relevant prey species (i.e. skipjack or yellowfin) were
262 absent in all stomach samples.

263 We tested the candidate models separately for the two stages of the mixture
264 model (Equations 1 and 2). In general, the set of candidate models were the same
265 between the binomial component (Equation 1) and the Gaussian component (Equation 2).
266 There were a few exceptions due to limited data for the Gaussian part of the model. The
267 data set "1955-1960" (see Supporting Information Appendix S1) and the gear type "pole
268 and line" were not included as variables in the models for skipjack tuna due to low
269 sample numbers. The GLMMs were fitted using the *glmer* function in the lme4 package
270 in R (R Development Core Team 2010) and model selection was based on Akaike
271 Information Criterion (AIC; Akaike 1973, Burnham & Anderson 2002). For each
272 modeling framework, we deemed candidate models with ΔAIC value less than 3 (i.e.
273 within 3 units of the lowest AIC model) to have substantial support based on the data.

274 Finally, we generated standardized diet fractions for each predator. These
275 estimates describe the proportional contribution by mass that skipjack and yellowfin tuna
276 comprise for each predator taxon/taxa, standardizing for location, set type and other
277 potential covariates. First, we predicted the occurrence ($\hat{y}$) and conditional proportion by

278 mass (û) of tunas in predator diets based on the best-fitting models. We then multiplied
279 the predicted values from the two stages to determine the expected proportion by mass of
280 skipjack and yellowfin tunas in predator diets ($\hat{C}$):

281 $$\hat{C} = \hat{y} \cdot \hat{u} \quad (3)$$

282

283 Broad comparisons of predator diets

284 We made broad comparisons of predation on skipjack and yellowfin tunas across
285 predator taxon/taxa for the entire tropical Pacific Ocean to evaluate the generality of the
286 results gleaned from the analysis of primary data from the eastern tropical Pacific Ocean.
287 Using the summarized published diet data, we calculated the mean frequency of
288 occurrence and proportional contribution by mass of tunas to the diets of sharks,
289 billfishes, yellowfin tuna, skipjack tuna, and other tuna species (Table 2, see also
290 Supporting Information Table S1 and Appendix S1). Other tunas included albacore
291 (*Thunnus alalunga*), bigeye (*Thunnus obesus*) and Pacific bluefin (*Thunnus orientalis*)
292 tunas. All predator taxon/taxa included in this analysis are listed in Table 2. We also
293 made regional comparisons of predation, by mean frequency of occurrence, on skipjack
294 and yellowfin tunas: summarized food habits data were not available for sharks and
295 skipjack in all three regions of the tropical Pacific Ocean (i.e. eastern, central and
296 western, Table 2).

297

298 Prey sizes and reproductive potential

299 We identified the sizes at which skipjack and yellowfin tunas were vulnerable
300 to predation by apex predators in the eastern tropical Pacific Ocean from the primary

food habits data. Estimates of individual prey body sizes consumed by individual predators were recorded during the contemporary sampling periods only (1992-1994 and 2003-2005). Fork lengths were measured for 45 skipjack tuna and 66 yellowfin tuna. We calculated the means and 95% confidence intervals of the sizes of skipjack and yellowfin tunas consumed by sharks, billfishes, and large-bodied tunas.

We estimated the relative reproductive potential of the skipjack and yellowfin tunas that are at the age / size most commonly consumed by apex predators. Reproductive potential is defined as the expected number of eggs that an individual of a particular age would produce over its remaining lifetime, given that it has already survived to that age (Gotelli 2001). This value is a function of the fecundity and survivorship of a fish at the different stages of its remaining life, and we present estimates for each length class relative to the maximum estimate of reproductive potential.

The reproductive potential (v) was calculated for all age / size classes x (Gotelli 2001) as:

$$v(x) = \frac{\sum_{y=x+1}^{k} l(y)b(y)}{l(x)}$$

where, $b(y)$ is the fecundity of an individual at age x or older, and $l(y)$ is annual survivorship for an individual at x older, and $l(x)$ is annual survivorship for an individual at age x. Essentially, we generated estimates of reproductive potential under unexploited conditions by taking virgin recruitment and using the natural mortality rate to calculate numbers at age. The numbers at age were then multiplied by fecundity at age and summed to get total reproductive potential of an unexploited stock. Here, $b(y)$ was

calculated using age-specific estimates of fecundity, proportion of females (sex ratio), and the percentage of females that are mature (see Supporting Information Table S2). Estimates of $l(x)$ were calculated from estimated age-specific natural mortality rates for combined male and female skipjack (Maunder and Harley 2005) and yellowfin tunas (Maunder and Aires-da-Silva 2009; see Supporting Information Table S2). These estimates are taken from the official stock assessments for these species and are supported by tagging data (Hampton 2000). We recognize that fishing is a large source of mortality on skipjack and yellowfin tunas, and that relative reproductive potential of smaller tunas will be different under exploitation. For instance, if the fishery targets tunas that are larger than those consumed by predators we may expect that the relative reproductive potential of the tunas being predated on will increase compared to those of larger-sized tunas. However, fishing is highly variable in intensity and selectivity and the reproductive potential of individual tunas is sensitive to estimates of mortality at age. Thus, to generate more stable estimates of tuna reproductive potential we modeled reproductive value under unexploited conditions. The parameter values used in our analysis were obtained from previously published literature and stock assessment reports (Schaefer 1998, Maunder & Harley 2005, Maunder 2007, Maunder & Aires-da-Silva 2009). Sex-specific information and estimates of fecundity were not available for Pacific skipjack tuna, so fecundity at age was assumed to be proportional to weight at age. This is a standard assumption in fisheries stock assessment and is used in a majority of assessments. We converted the estimates of reproductive potential at each age class to estimates at length using published length at age relationships for skipjack (Bayliff 1988) and yellowfin (Wild 1986) tunas.

346

347 **Results**

348 Tunas in predator diets

349 The frequency of occurrence of skipjack and yellowfin tunas in predator stomach
350 samples were best predicted by models that included only predator taxon/taxa and
351 set/gear type (Model 6; Table 1). For skipjack tuna, the model with predator taxon/taxa,
352 location of capture, and fishing set/gear type as predictors also fit the data well (Model
353 11; Table 1). For yellowfin tuna, the model with only predator taxon/taxa as a predictor
354 variable (Model 1) performed nearly as well as the best fitting model (Model ΔAIC =
355 0.07). The coefficients of the best-fitting models indicate that the frequency of predation
356 on both species was greatest in floating-object sets, intermediate for dolphin sets, and
357 lowest in the unassociated school sets and pole-and-line fisheries (See Supporting
358 Information Table S3 for detailed listing of model coefficients). Dataset was not included
359 in the best-fitting models for skipjack and yellowfin tunas, which suggests that the
360 occurrence of these tunas in predator diets did not change over time or that a change
361 could not be detected based on the available data.

362 We identified the predators that had the highest probability of consuming skipjack
363 and yellowfin tuna based on model coefficients from these best-fitting models. We found
364 that skipjack tuna were most frequent in the diets of blacktip sharks (*Carcharhinus*
365 *limbatus*), silky sharks (*Carcharhinus falciformis*), Indo-Pacific sailfish (*Istiophorus*
366 *platypterus*), and marlins (*Makaira* spp.) and were least frequent in the diets of spotted
367 dolphins (*Stenella attenuata*), yellowfin tuna, and dolphinfish (*Coryphaena hippurus*). Of
368 the large pelagic fishes and tunas, requiem sharks (*Carcharhinus* spp.), hammerhead

sharks (*Spyrna* spp.), and marlin (*Makaira* spp.) were most likely to consume yellowfin tuna while large-bodied conspecifics were the least likely to consume them (see Supporting Information Table S3). Several species were never found to have consumed skipjack or yellowfin tunas (primary data): bigeye tuna (*Thunnus obesus*), black skipjack tuna (*Euthynnus lineatus*), skipjack tuna (*Katsuwonus pelamis*), and spinner dolphin (*Stenella longirostris*).

The conditional percent mass contribution of skipjack and yellowfin tunas were best predicted by capture method alone. Generally, skipjack and yellowfin tunas comprised the greatest proportion of predator diets in unassociated and floating-object sets, compared to other fishing methods (see Supporting Information Table S3).

Standardized diet fractions (proportion of predator diet, by mass, consisting of skipjack and yellowfin tuna) were highest for sharks and marlins (Fig. 2). The expected proportion by mass of blacktip sharks diets composed on skipjack tuna was approximately 47%. For yellowfin tuna, the expected proportions by mass reached nearly 40% and 18% of shark and marlin diets, respectively (Fig. 2). Moreover, the standardized diet fractions indicate that skipjack and yellowfin tuna were a more important prey for predators captured in floating-object sets compared to the other fishing methods (estimates based on the center of the sampling distribution; Fig. 2). Standardized diet fractions by predator and set/gear type were estimated only when at least three predators of the same species were captured in a given set/gear type.

Broad comparisons of predator diets

391 The compilation of summarized diet data from locations throughout the tropical
392 Pacific Ocean confirmed the importance of skipjack and yellowfin tunas in the diets of
393 large-bodied predators found in the eastern Pacific Ocean (Fig. 3), and also revealed
394 potential regional differences in predation on these tuna species (Fig. 4). Overall, the
395 frequency of occurrence of skipjack tuna in predator diets was greatest for billfishes.
396 Skipjack tuna also comprised a considerable portion of sharks' diets and the diets of
397 large-bodied yellowfin tuna and conspecifics (Fig. 3). This finding differs from our
398 analysis of the primary data for the eastern Pacific alone, which suggested that sharks
399 consumed skipjack tuna more often than do billfishes and that there was little to no
400 predation on skipjack by conspecifics or other tuna species. This discrepancy could be
401 attributed to regional differences in predation. Our analysis of the summarized data
402 revealed a higher occurrence of skipjack tuna in the diets of large-bodied yellowfin tuna
403 and conspecifics in the western and central regions of the Pacific Ocean compared to the
404 eastern region (Fig. 4). This regional gradient of predation was also observed for sharks
405 and was particularly notable for billfishes (Fig. 4). The occurrence of skipjack in billfish
406 diets was as much as 40% and 30% in the western and central Pacific Ocean,
407 respectively, whereas the highest estimate of occurrence in the eastern region was
408 approximately 3% (*Makaira nigricans*).
409 Over all regions of the tropical Pacific Ocean, the frequency of occurrence of
410 yellowfin tuna in predator diets was greatest for sharks and billfishes and least for large-
411 bodied conspecifics and other tuna species (Fig. 3). This finding is consistent with our
412 analysis of primary data from the eastern tropical Pacific Ocean. The summarized diet
413 data did not reveal a regional gradient of predation on yellowfin tuna by large-bodied

predators, however there are regional differences. Similar to our findings for skipjack tuna, the occurrence of predation on yellowfin tuna by billfishes was greatest in the western tropical Pacific Ocean compared to the central and eastern regions (Fig. 4).

Prey sizes and reproductive potential

Large-bodied predators consumed a wide size range of tunas, ranging from early life stages to sub-adults. Predators consumed skipjack tuna with body sizes up to 80 cm in length (Fig. 5). The mean lengths of skipjack tuna consumed by billfish, sharks, and tunas were 26 cm, 27 cm, and 19 cm, respectively. The maximum size of yellowfin tuna consumed by predatory fishes was approximately 100 cm in length and the mean body sizes of yellowfin tuna consumed by billfish, sharks, and tunas were 45 cm, 37 cm, and 22 cm, respectively (Fig. 5).

Because large predatory fishes preyed upon a wide size range for both skipjack and yellowfin tunas, the reproductive potential of individuals that were consumed also ranged widely (Fig 5). For both species we found predation on size classes that had notable reproductive potential (Fig. 5). Reproductive potential in skipjack tuna is maximized at approximately age 1.5 years (body length = 60 cm), while for yellowfin tuna it is greatest at age 3 (body length =125 cm). Approximately 13% of all the skipjack tuna found in predator stomachs had reproductive potential that exceeded 20% of the maximum. Similarly, 15% of all yellowfin tuna found as prey had reproductive potential that exceeded 20% of the maximum. For some predator taxon/taxa, this was greater: sharks and billfishes consumed skipjack and yellowfin tunas with estimated ages that had reproductive potentials as great as 60% of the maximum (Fig. 5). Evidence of a single

437 >70 cm skipjack tuna and four >100 cm yellowfin tuna in the stomachs of sharks (Fig. 5)
438 suggests that top predators are also capable of consuming larger tunas that have even
439 higher reproductive value. We note that the overall trend of relative reproductive
440 potential was the same when we used estimates of fecundity for Indian Ocean skipjack
441 tuna (from Stéquert & Ramcharrun 1995) in our calculations.
442

443 **Discussion**
444
445 Tropical tunas, particularly yellowfin tuna, are often considered apex predators in
446 pelagic food webs in the Pacific Ocean. However, our findings suggest that tropical tunas
447 at large body sizes are consistently preyed upon by a guild of large-bodied predators, and
448 therefore are better considered mesopredators. Both a detailed analysis of primary data
449 collected in a single, large region and a synthesis of previously published diet studies
450 throughout the tropical Pacific Ocean support the hypothesis that these tropical tunas
451 comprise a substantial component of the diet of sharks and billfishes. Although much of
452 this predation was directed at very small-sized tunas–a pattern of ontogenetic predation
453 risk not uncommon among marine fishes–we find that predation also extends to later life
454 history stages, including those that have significant reproductive value. Thus, predation
455 by sharks and billfishes has the potential to play an important role in regulating skipjack
456 and yellowfin tuna populations. The question of top-down control on tropic tunas remains
457 to be answered, but our work provides future research efforts with essential knowledge
458 about potentially important predators on tunas and size vulnerability of predation.
459 The possibility that sharks and billfishes could regulate tropical tunas raises two
460 questions. The first is whether current levels of skipjack and yellowfin tuna productivity

461 may have been fostered by the reduction of large-bodied predators by industrial fishing
462 (Ward & Myers 2005). For example, if tropical tunas are indeed regulated in part by
463 these predators, the high levels of skipjack tuna productivity observed over the past
464 decade (e.g. Sibert et al. 2006) could represent a shifting baseline (Pauly 1995, Pinnegar
465 & Engelhard 2008). A second, related question is whether the potential recovery of
466 sharks and billfishes might lead to secondary effects on skipjack and yellowfin tunas.
467 Fishing can modify the structure and functioning of marine systems (see Baum & Worm
468 2009), and increasing efforts are being made to foster a rebuilding of shark (Gallucci et
469 al. 2006, Watson et al. 2009) and billfish (Kitchell et al. 2004, Kerstetter & Graves 2006,
470 Kaplan et al. 2007, Pine et al. 2008) populations. Recovery of depleted species can have
471 surprising consequences when there are high interaction strengths between exploited
472 species. For instance, the recovery of Barents Sea cod coupled with fishing on their prey,
473 capelin, contributed to a collapse in the capelin population (Hjermann et al. 2004), which
474 subsequently recovered. Unlike capelin, tunas are not considered "forage" species;
475 however the interaction strengths among tunas and their predators need not be symmetric
476 for strong top-down interactions. For example, sharks and billfishes might still play a role
477 in regulating these tunas even though they may not relay on tunas as an essential diet
478 item. If these fishes do exert consumer control on skipjack and yellowfin tunas, a
479 recovery of these large predators could potentially alter the productivity of highly-valued
480 tuna species.

481 The concept of mesopredator release has received much attention in recent years
482 (e.g. Elmhagen and Rushton 2007, Prugh et al. 2009, Baum & Worm 2009, Ritchie &
483 Johnson 2009, Brashares et al. 2010). While most studies of this ecological phenomenon

484 are based in terrestrial and coastal marine ecosystems, there is accumulating evidence of
485 this process in oceanic ecosystems. For instance, both short (Polovina et al. 2009) and
486 long-term (Ward & Myers 2005) changes in longline catch rates of mid- and high-trophic
487 level pelagic fishes support the possibility of mesopredator release. Also, Worm and
488 Tittensor (2011) suggest that increases in the number and range of skipjack tuna in the
489 eastern tropical Pacific could be attributed to depletion of large-bodied tunas, sharks, and
490 marlins. By identifying predator species that are most capable of exerting top-down
491 control and the vulnerability of tunas by size to predation, our analyses provide a strong
492 foundation to better explore the extent by which large-bodied apex predators, particularly
493 sharks and marlins, might impact tuna populations.

494 Identifying whether shark and billfish species do indeed regulate tuna through
495 predation processes is a challenging task. A strong top-down interaction is likely if a
496 predator represents an important source of total mortality on tunas and if the predation
497 mortality strongly depends on predator abundance (Essington and Hansson 2004). An
498 evaluation of whether these two criteria are met requires knowledge of predator feeding
499 rates on tuna life stages as well as predator and prey relative abundances. This
500 information is not available for many oceanic predators due to the sampling and data
501 challenges associated with open ocean ecosystems (Baum and Worm 2009).
502 Consequently, attempts to identify consumer control within these systems have been
503 limited. A food web model of the north Pacific subtropical gyre has been used to evaluate
504 the trophic impacts of predator removals on food web components in this region (Kitchell
505 et al. 1999, 2002; Cox et al. 2002). Some model scenarios did not reveal evidence of
506 mesopredator release in response to fisheries removals of apex predators (Kitchell et al.

2002), while others suggested that increased biomass of small tropical tunas, particularly yellowfin tuna, resulted from reduced predation by sharks and billfishes (Cox et al. 2002). Large food web models are often fit to fishery-dependent data, and therefore are limited by the large uncertainties associated with the vagaries introduced by non-constant catchability and spatial dynamics of fishing fleets (Walters 2003; Maunder et al. 2006).

The question of top down control of tropical tunas remains to be answered. Future work is needed to evaluate how skipjack and yellowfin may respond to changes in predator abundances and whether trophic interactions need to be accounted for more explicitly in the assessments of these tuna species. Our study provides a detailed analysis of predator-prey interactions and knowledge about potentially important predators on tunas and vulnerability by size to predation. We envision a potential next step as one that incorporates our findings in an age-structured population-modeling framework to assess the impacts that sharks and billfishes have on stock productivity under various levels of predation mortality. Also, tropical tunas, especially yellowfin tuna, interact with these apex predators through competition for shared prey resources, therefore mechanisms of competition need to be addressed when modeling the population dynamics of tunas under increased predation. An important consideration in future analyses will be the calculation of the range in common biological reference points that can be attributed to changes in predator stocks. This information can then be used to further evaluate whether diminished levels of large pelagic fishes have enhanced the production of tuna stocks. Alternatively, reductions in apex predators could lead to increased competition and (or) increased predation on tunas from other species.

529 The role of cannibalism in the population dynamics and persistence of tropical
530 tunas, particularly skipjack tuna, also warrants further attention. Cannibalism is
531 widespread in marine fish populations, and can represent a major source of mortality on
532 juvenile fishes (Smith & Reay 1991). Cannibalism can serve as a density-dependent
533 mechanism for population regulation (Anderson & Gregory 2000, Wespestad et al. 2000,
534 Neuenfeldt & Koster 2000), while also providing a source of nutrition to adult fishes
535 when alternative food sources are lacking. Through our analysis of summarized food
536 habits data we found a notable occurrence of conspecifics in the diet of skipjack tuna.
537 Our estimates of skipjack cannibalism are not as high as those for some marine fishes
538 (e.g. gadoids, see Juanes 2003). However, skipjack tuna have high consumption and
539 production rates and high biomass; they are the most abundant of the assessed predator
540 stocks in the tropical Pacific Ocean. Thus, adult conspecifics could have a substantial
541 impact on the recruitment of juvenile fishes and act as an important structuring force on
542 the population, even if the juveniles comprised only a small component of the adult diet.
543 Yellowfin tuna appeared to be minor predators on themselves. A low occurrence of
544 yellowfin tuna cannibalism is not surprising because the adults are known to feed mainly
545 near the thermocline, while the larval and juvenile stages occupy surface waters (see
546 Longhurst 2010). The frequency and quantity of yellowfin tuna predation on skipjack
547 tuna was considerable, although yellowfin tuna consumed only small-sized skipjack and
548 conspecifics that have less reproductive potential because of cumulative mortality prior to
549 spawning. If large-bodied tunas do have a predation effect on skipjack and yellowfin
550 tunas it is likely to act primarily on pre-recruits and to be manifested through recruitment
551 (i.e. age at which tunas are first vulnerable to fishing gear).

552 An interesting outcome of our work is the evidence of a possible gradient of
553 predation on skipjack tuna by large predators between the eastern and western tropical
554 Pacific Ocean. This finding is supported by previous evidence that suggests that skipjack
555 tuna is a major prey item of conspecifics and top predators in western and central regions
556 of the tropical Pacific Ocean (Allain et al. 2007) and is less important as prey in the
557 eastern region (Olson & Watters 2003). This trend could arise due to regional differences
558 in productivity and prey availability. For example, the eastern tropical Pacific Ocean has
559 large upwelling regions (Fiedler and Tallet 2006) and thereby is highly productive and
560 supports a large biomass and size spectrum of forage items, including epipelagic fishes
561 and small scombrids (e.g. frigate and bullet tunas) that are consumed by top predators. In
562 comparison, the central and western regions are less productive, and thus we may expect
563 that the availability and biomass of mid-trophic level prey species is much lower in these
564 areas. If this is true, then sharks, marlins, and large-bodied tunas are likely to depend
565 more heavily on the large biomass of skipjack tuna for sustenance in the central and
566 western tropical Pacific Ocean than in the eastern region, where there are many
567 alternative prey items. The gradient of predation could also be attributed to the spatial
568 distribution of skipjack tuna. For example, according to the catch of purse seine and pole-
569 and-line fisheries, larger-sized skipjack tuna are more abundant in the central Pacific
570 Ocean compared to the western Pacific Ocean (Hoyle et al. 2010). If the mean sizes of
571 skipjack tuna do indeed increase eastward across the Pacific Ocean, then predation on
572 these tunas may be more limited by body size constraints in the eastern region compared
573 to the central and western regions.

574 Our analysis revealed that predation on tunas by large pelagic fishes sampled
575 from purse-seine floating-object sets (primarily FADs) was greater than for those
576 captured via other methods. Specifically, capture method was an important predictor of
577 both the frequency of occurrence and conditional percent mass contribution for both
578 skipjack and yellowfin tunas. In all cases, the occurrence of predation was found to be
579 strongest from samples collected in floating-object sets, suggesting that floating objects
580 may potentially modify the pelagic habitat by aggregating small-sized skipjack,
581 yellowfin, and bigeye tunas and thereby enhancing their vulnerability to predators. It is
582 plausible that capture method might also explain some of the discrepancies in predation
583 intensity estimated from primary and summarized data. For example, the summarized
584 data for sharks and marlins are mostly based on predators captured in local, artisanal
585 fisheries and not by commercial fishing methods. However, differences in predator
586 species composition and capture locations that comprise the primary and summarized
587 data could contribute to the discrepancies as well. Previous authors (e.g. Dempster &
588 Taquet 2004) have voiced concern over the ecological consequences of deploying large
589 numbers of FADs to target highly-valued tunas. Our analysis supports a hypothesis that
590 the use of floating-object sets in pelagic fisheries could be altering trophic interactions
591 and feeding patterns in a way that increases predation pressure on small-bodied tunas.
592

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References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrova, BN, Csaki, F (eds) Proceedings of the 2nd International Symposium on Information. Publishing House of the Hungarian Academy of Sciences, Budapest.

Allain V, Nicol S, Essington TE, Okey TA, Olson RJ Kirby DS (2007) An Ecopath with Ecosim model of the Western and Central Pacific Ocean warm pool pelagic ecosystem. 3rd Meeting of the Scientific Committee of the Western and Central Pacific Fisheries Commission, WCPFC-SC3, Honolulu, Hawaii, USA, EB SWG/IP-8, p 1-42

Alverson FG (1963) The food of yellowfin and skipjack tunas in the Eastern Tropical Pacific Ocean. Inter-Am Trop Tuna Comm Bull 7:293-367

Anderson JT, Gregory RA (2000) Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. ICES J Mar Sci 57:349-359

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the Northwest Atlantic. Science 299:389-392

Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundance. J Anim Ecol 78:699-714

Bayliff WH (1988) Growth of skipjack, *Katsuwonus pelamis*, and yellowfin, *Thunnus albacares*, tunas in the eastern Pacific Ocean as estimated from tagging data. Inter-Am Trop Tuna Comm Bull 19:307-385

Brashares JS, Prugh LR, Stoner CJ, Epps CW (2010) Ecological and conservation implications of mesopredator release. In: Terborgh J, Sough M (eds) Trophic

Cascades: predators, prey, and the changing dynamics of nature Island Press, Washington, D.C., p 221-240

Brock RE (1984) A contribution to the trophic biology of the blue marlin (*Makaira nigricans* Lacépéde, 1802) in Hawaii. Pac Sci 38:141-149

Burnham KP, Anderson, DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, USA

Caddy JF, Seijo JC (2002) Reproductive contributions foregone with harvesting: a conceptual framework. Fish Res 59:17-30.

Cortes E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707-717

Cox SP, Essington TE, Kitchell JF, Martell SJD, Walters CJ, Boggs C, Kaplan I (2002) Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952-1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. Can J Fish Aquat Sci 59:736-1747

Crouse DT, Crowder LB, Caswell H (1987) A stage-based population-model for loggerhead sea-turtles and implications for conservation. Ecology 68:1412-1423

Daan N, Gislason H, Pope JG, Rice JC (2005) Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES J Mar Sci 62:177-188

Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. PNAS 104:10518-10523

Dempster T, Taquet M (2004) Fish aggregation device (FAD) research: gaps in current knowledge and future directions for ecological studies. Rev Fish Biol Fish 14:21-42

Elmhagen B, Rushton SP (2007) Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol Lett 10 197-206

Essington TE (2010) Ecological indicators display reduced variation in North American catch share fisheries. PNAS 107:754-759

Essington TE, Hansson S (2004) Predator-dependent functional response and Interaction strengths in a natural food web. Can J Fish Aquat Sci 61:2227-2236

Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282: 473-476

Fiedler, PC, Talley LD (2006) Hydrography of the eastern tropical Pacific: a review. Prog Oceanogr 69: 143-180

Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621-1623

Gallucci VF, Taylor IG, Erzini K (2006) Conservation and management of exploited shark populations based on reproductive value. Can J Fish Aquat Sci 63:931-942

Gelman A, Hill J (2007) Data analysis using regression and multilevel / hierarchical models. Cambridge University Press, Cambridge UK

Gotelli NJ (2001) A primer of ecology. Sinauer Associates, Sunderland, Massachusetts, USA

Hampton J (2000) Natural mortality rates in tropical tunas: size really does matter. Can J Fish Aquat Sci 57:1002-1010

Hjermann DØ, Ottersen G, Stenseth NC (2004) Competition among fishermen and fish causes the collapse of Barents Sea capelin. PNAS 101:11679-1168

Hoyle S, Kleiber P, Davies N, Harley S, Hampton, J (2010) Stock assessment of skipjack tuna in the Western and Central Pacific Ocean. WCPFC-SC6-2010/SA-WP-10. 10–19 August 2010. Nuku'alofa, Tonga

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629-638

Jensen OP, Seppelt R, Miller TJ, Bauer LJ (2005) Winter distribution of blue crab (*Callinectes sapidus*) in Chesapeake Bay: Application and cross-validation of a two-stage generalized additive model (GAM). Mar Ecol Prog Ser 299:239-255

Juanes F (2003) The allometry of cannibalism in piscivorous fishes. Can J Fish Aquat Sci 60:594-602

Kaplan IC, Cox SP, Kitchell JF (2007) Circle hooks for Pacific longliners: Not a panacea for marlin and shark bycatch, but part of the solution. Trans Am Fish Soc 136:392-401

Kerstetter DW, Graves JE (2006) Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery. Fish Res 80:239-250

King JE, Ikehara II (1956) Comparative study of food of bigeye and yellowfin tuna in the central pacific. Fish Bull 57:61-85

Kitchell JF, Boggs C, He X, Walters CJ (1999) Keystone predators in the Central Pacific. In: Ecosystem approaches to fisheries management. University of Alaska Sea Grant. AL-SG-99-01, p 665-683

Kitchell JF, Essington TE, Boggs CH, Schindler DE, Walters CJ (2002) The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. Ecosystems 5:202-216

Kitchell, J.F., Kaplan, I.C., Cox, S.P., Martell, S.J.D., Essington, T.E., Boggs, C.H. & Walters, C.J. (2004) Ecological and economic components of alternative fishing methods to reduce by-catch of marlin in a tropical pelagic ecosystem. Bull Mar Sci 74:607-619

Longhurst A (2010) Mismanagement of Marine Fisheries. Cambridge University Press, Cambridge, UK.

Maunder MN (2007) Status of skipjack tuna in the eastern Pacific Ocean in 2006 and outlook. Inter-Am Trop Tuna Comm Stock Assess Rep 8, La Jolla, California, USA

Maunder MN, Aires-da-Silva A (2009) Status of yellowfin tuna in the eastern Pacific Ocean in 2007 and outlook for the future. Inter-Am Trop Tuna Comm Stock Assess Rep 9, La Jolla, California, USA

Maunder MN, Harley SJ (2005) Status of skipjack tuna in the eastern Pacific Ocean in 2003 and outlook for 2004. Inter-Am Trop Tuna Comm Stock Assess Rep 5, La Jolla, California, USA

Maunder MN, Sibert JR, Fonteneau A, Hampton J, Kleiber P, Harley S (2006) Interpreting catch-per-unit-of-effort data to assess the status of individual stocks and communities. ICES J Mar Sci 63:1373-1385

Maunder MN, Punt AE (2004) Standardizing catch and effort data: a review of recent approaches. Fish Res 70:141–159

Minami M, Lennert-Cody C, Gao W, Román-Verdesoto M (2007) Modeling shark bycatch: The zero-inflated negative binomial regression model with smoothing. Fish Res 84:210-221

Neuenfeldt S, Köster FW (2000) Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. ICES J Mar Sci 57:300-309

Olson R, Watters G (2003) A model of the pelagic ecosystem in the estaern tropical Pacific Ocean. Inter-Am Trop Tuna Comm Bull 22:135-218

Pauly D (1995) Anecdotes and the shifting baseline syndrome in fisheries. Trends Ecol Evol 10:430

Pine WE, Martell SJD, Jensen OP, Walters CJ, Kitchell JF (2008) Catch-and-release and size limit regulations for blue, white, and striped marlin: the role of post release survival in effective policy design. Can J Fish Aquat Sci 65:975-988

Pinnegar JK, Engelhard GH (2008) The 'shifting baseline' phenomenon: a global perspective. Rev Fish Biol Fish 18:1-16

Polovina JJ, Abecassis M, Howell EA, Woodworth P (2009) Changes among trophic levels in the central North Pacific subtropical gyre ecosystem, 1996-2000. Fish Bull 107:523-531

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The rise of the mesopredator. Bioscience 59:779-791

R Development Core Team (2009) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reum JCP, Essington TE, Greene CM, Rice CA, Fresh KL (2011) Multiscale influence of climate on estuarine populations of forage fish: the role of coastal upwelling, freshwater flow and temperature. Mar Ecol Prog Ser 425:203-215

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982-988

Schaefer KM (1998) Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Inter-Am Trop Tuna Comm Bull 21:205-272

Schindler DE, Essington TE, Kitchell JF, Boggs C, Hilborn R (2002). Sharks and Tunas: Fisheries Impacts on Predators with Contrasting Life Histories. Ecol Appl 12:735-748

Seki MP, Polovina JJ (2001) Ocean gyre ecosystems. In: Steele JH, Thorpe SA, Turekian, KK (eds) The Encyclopedia of Ocean Sciences, Vol 4. Academic Press, San Diego, California, USA, p 1959-1964

Sibert J, Hampton J, Kleiber P, Maunder M (2006) Biomass, size, and trophic status of top predators in the Pacific Ocean. Science 314:1773-1776

Smith C, Reay P (1991) Cannibalism in teleost fish. Rev Fish Biol Fish 1:41-64.

Stéquert B, Ramcharrun B (1995) Fecundity of skipjack tuna (*Katsuwonus pelamis*) from the Western Indian Ocean. Aquat Living Res 8:79-89

Wallace BP, Heppell SS, Lewison RL, Kelez S, Crowder LB (2008) Impacts of fisheries bycatch on loggerhead turtles worldwide inferred from reproductive value analyses. J Appl Ecol 45:1076-1085

Wallace BP, Lewison RL, McDonald SL, McDonald RK, Kot CY, Kelez S, Bjorkland RK, Finkbeiner EM, Helmbrecht S, Crowder LB (2010) Global patterns of marine turtle bycatch. Cons Lett 3:131-142

Walters C (2003) Folly and fantasy in the analysis of spatial catch rate data. Can J Fish Aquat Sci 60:1433-1436

Ward P, Myers RA (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology 86:835-847

Watson JT, Essington TE, Lennert-Cody CE, Hall MA (2009) Trade-offs in the design of fishery closures: management of silky shark bycatch in the eastern Pacific Ocean tuna fishery. Cons Biol 23:626-635

Wespestad VG, Fritze LW, Ingraham WJ, Megrey BA (2000) On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye pollock (*Theragra chalcogramma*). ICES J Mar Sci 57:272-278

Wild A (1986) Growth of yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific Ocean based on otolith increments**.** Inter-Am Trop Tuna Comm Bull 18: 421-482

Williams TM, Estes JA, Doak DF, Springer AM (2004) Killer appetites: assessing the role of predators in ecological communities. Ecology 85:3373–3384

Worm B, Tittensor DP (2011) Range contraction in large pelagic predators. Proc Nat

Acad Sci 108:11942-11947

Worm B, Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84:162-173

Zar JH (1999) Biostatistical Analysis. Prentice Hall, EngleWoood Cliffs, New Jersey, USA.

Supporting Information

The following Supporting Information is available for this article online.

Appendix S1. Description of the primary data used in the study.

Table S1. List of theses, reports, and peer-reviewed publications from which summarized food habits data in the eastern tropical Pacific Ocean were obtained.

Table S2: Data used to estimate the reproductive potential of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean.

Table S3. Maximum likelihood estimates of fixed effects in the best fitting generalized linear mixed models for skipjack and yellowfin tuna.

Appendix S2. References for theses, reports, and peer-reviewed publications from which summarized food habits data in the eastern tropical Pacific Ocean were obtained.

Table 1: Candidate models used to identify the frequency of occurrence and conditional percent mass contribution of skipjack (SKJ) and yellowfin (YFT) in the diets of apex predators in the eastern Tropical Pacific Ocean based on primary food habits data. The fixed effects, number of parameters (K), and ΔAIC values (AIC values – minimum AIC value) for the generalized linear mixed models are shown. The numbers of estimated parameters (K) in YFT models are denoted in parentheses. Each model included an intercept and random effect term (fishing set ID).

		Frequency of occurrence			Composition by mass		
ID	**Candidate Models**	**K**	**ΔAIC_{SKJ}**	**ΔAIC_{YFT}**	**K**	**ΔAIC_{SKJ}**	**ΔAIC_{YFT}**
1	Predator	13 (11)	11	0.07	14 (12)	28	16
2	Lat + Lon + Area	7	115	198	8	7	19
3	DataSet + Season	8	122	202	8 (9)	14	29
4	Set/Gear	5	85	175	5 (6)	**0**	**0**
5	Predator + Lat + Lon + Area	18(16)	3	4	19 (17)	30	33
6	Predator + Set/Gear	16 (14)	**0**	**0**	16 (15)	22	22
7	Predator + DataSet + Season	19 (17)	9	5	19 (18)	35	28
8	Lat + Lon + Area + Set/Gear	10	85	178	10 (11)	7	18
9	Lat + Lon + Area + DataSet + Season	13	106	193	13 (14)	18	43
10	Set/Gear + DataSet + Season	11	88	177	10 (12)	14	23
11	Predator + Lat + Lon + Area + Set/Gear	21 (19)	1	5	21 (20)	29	40
12	Predator + Lat + Lon + Area + DataSet + Season	24 (22)	7	6	24 (23)	40	44
13	Predator + Set/Gear + DataSet + Season	22 (20)	7	1	21 (21)	35	35
14	DataSet + Season + Lat + Lon + Area + Set/Gear	16	89	175	15 (17)	20	39
15	Predator + Lat + Lon + Area + Set/Gear + DataSet + Season	27 (25)	7	3	26	41	50

Table 2: List of the predators used in our analysis, the regions from which diet data have been collected for the respective predators, the type of data (summarized vs. primary data) available for each predator, and the total sample sizes of predators for each period in which primary data was collected. East, eastern tropical Pacific; Central, central tropical Pacific; and West, western tropical Pacific. [1]Included as level of predator categorical variable in GLMMs for yellowfin tuna. [2]Predators included in GLMMs for skipjack. nei = not elsewhere included.

Predator	Common name	West	East	Central	Summarized	Primary	1955-1960	1969-1972	1992-1994	2003-2005
Alopias pelagicus	Pelagic thresher shark		x		x	x				3
Alopias superciliosus	Bigeye thresher shark		x		x					
Alopias sp.	Thresher sharks, nei		x	x	x	x			9	
Carcharhinus falciformis [1,2]	Silky shark		x	x	x	x			256	319
Carcharhinus leucas	Bull shark		x		x	x			2	
Carcharhinus limbatus [2]	Blacktip shark		x			x			24	5
Carcharhinus longimanus [1,2]	Oceanic whitetip shark		x	x	x	x			15	6
Carcharhinus sp. [1,2]	Requiem sharks, nei		x			x			37	
Isurus oxyrinchus	Shortfin mako shark		x	x	x	x			3	2
Prionace glauca	Blue shark		x	x	x	x			1	
Sphyrna lewini [1]	Scalloped shark		x		x	x				2
Sphyrna zygaena	Smooth hammerhead shark		x		x	x			15	3
Sphyrna sp. [1,2]	Hammerhead sharks, nei		x			x			29	
Makaira indica [1,2]	Black marlin	x			x	x			22	2
Makaira nigricans [1,2]	Blue marlin		x	x	x	x			9	15
Makaira sp. [1,2]	Black marlin, blue marlin		x			x			1	
Istiophorus platypterus [2]	Indo-Pacific sailfish		x		x	x			47	2
Tetrapturus audax	Striped marlin		x		x	x			8	2
Tetrapturus angustirostris	Shortbill spearfish		x			x				1
Xiphias gladius	Swordfish		x		x					
Istiophoridae, Xiphiidae	Billfishes, nei	x		x	x					
Katsuwonus pelamis	Skipjack tuna		x	x	x	x			135	285
Thunnus albacares [1,2]	Yellowfin tuna	x	x	x	x	x	2272	3114	2895	1071
Thunnus alalunga	Albacore tuna	x	x	x	x	x				3
Thunnus obesus	Bigeye tuna	x	x	x	x	x			38	89
Thunnus orientalis	Pacific bluefin tuna		x		x	x				7
Thunnini	Tunas, nei	x		x	x					
Stenella attenuata [2]	Spotted dolphin		x		x	x			231	2
Coryphaena hippurus [1,2]	Common dolphinfish		x		x	x			41	353
Coryphaenidae[1]	Dolphinfishes		x			x			223	1
Seriola rivoliana [1,2]	Almaco jack		x			x				64
Elagatis bipinnulata [1,2]	Rainbow runner		x			x			32	194
Acanthocybium solandri [1,2]	Wahoo		x			x			113	480

Figure Captions

Figure 1: Sampling locations of predators for which primary data were available. Black circles, years 1955-1960; gray squares, years 1969-1972; open circles, years 1992-1994; open triangles, years 2003-2005.

Figure 2: Overlapping bar plot (all bars start at zero) of the predicted consumption of skipjack (SKJ) and yellowfin (YFT) tunas as a function of predator and fishing method. Predictions were generated from mixture models (also known as delta-normal or two stage hurdle model) fit to the frequency of occurrence and conditional mass (%) of tunas in predators' stomachs determined from primary food habits data. Set/gear types: unassociated sets (black), dolphin sets (white), and floating-object sets (light gray). We do not include predictions for pole-and-line because this fishing method was only used to capture yellowfin tuna during the historical period.

Figure 3: Mean contributions of skipjack (SKJ) and yellowfin (YFT) tunas in the diets of apex predators in the tropical Pacific Ocean. Mean estimates (+SD) are based on summarized data sources. The "Other tunas" category includes albacore, bigeye and Pacific bluefin tunas. Percent by frequency of occurrence, gray; percent by mass, black. NA; data not available.

Figure 4: Percent frequency of occurrence of skipjack (SKJ) and yellowfin (YFT) tunas in the diets of apex predators in the eastern (dark gray), central (light gray), and western (black) tropical Pacific Ocean. Mean estimates (+SD) are based on summarized data

sources. The “Other tunas” category includes albacore, bigeye and Pacific bluefin tunas. NA; data not available.

Figure 5: Frequency (number) of skipjack (SKJ) and yellowfin (YFT) tunas, by body size, consumed by sharks (dark gray bars), marlins (light gray bars), and large-bodied tunas (white bars) in the eastern tropical Pacific Ocean. The dashed black lines represent estimates of the relative reproductive potential of individual skipjack and yellowfin tunas across size classes. The solid black lines denote the body sizes that comprise 90% of tuna catches.

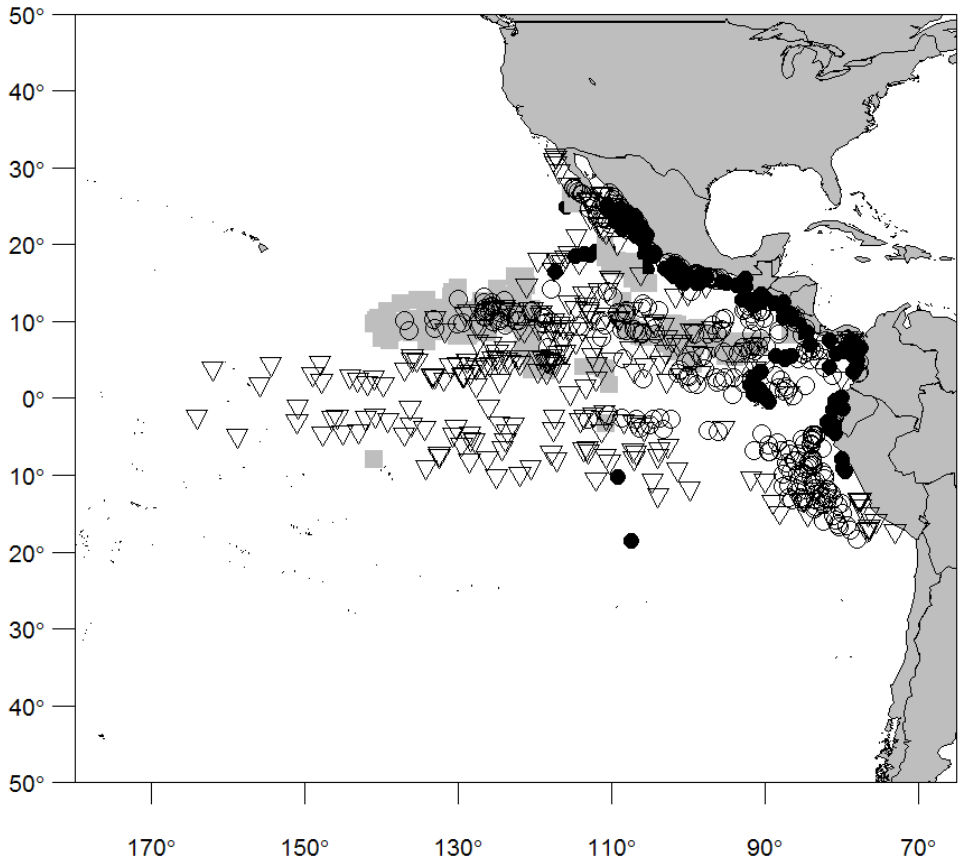

Fig. 1

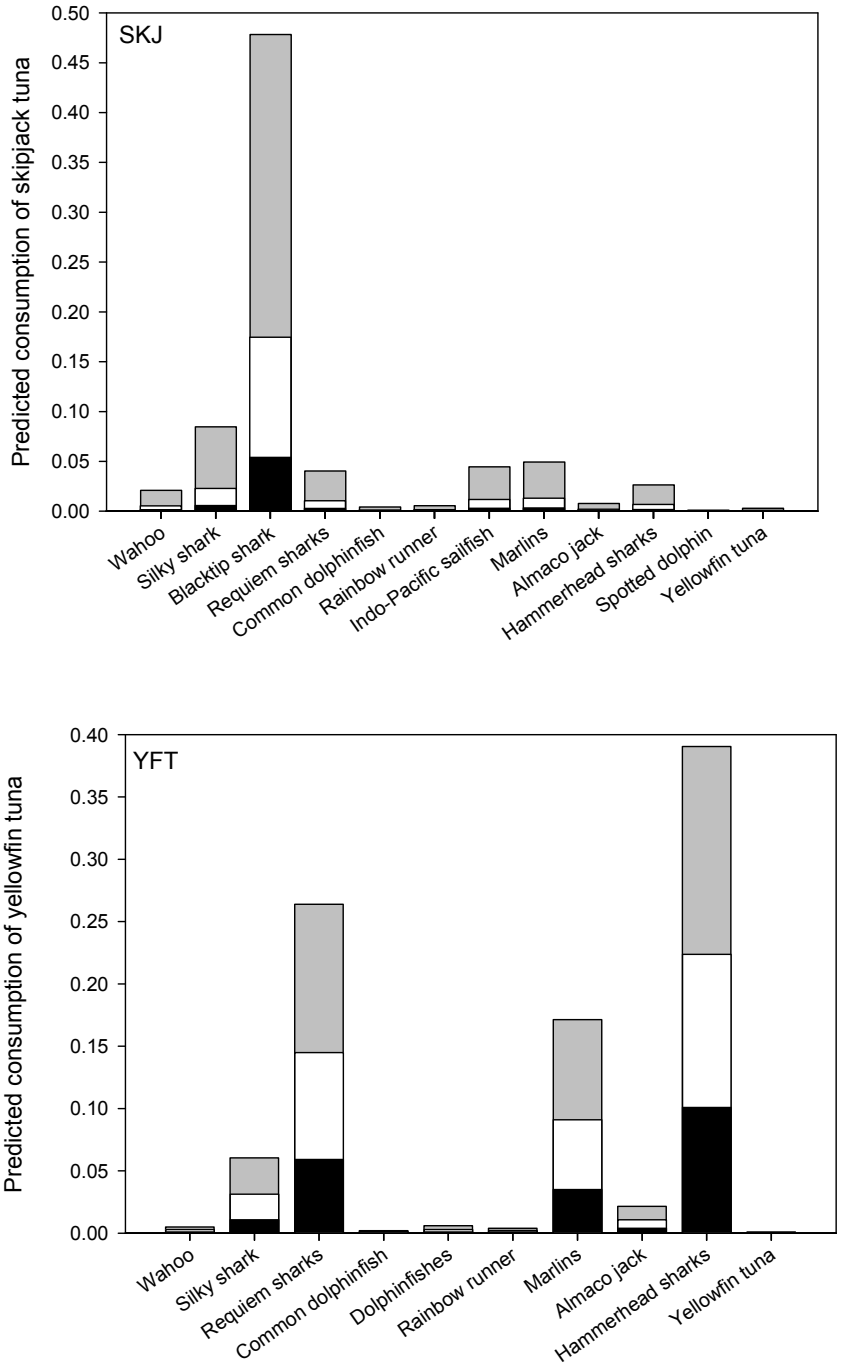
SKJ
Predicted consumption of skipjack tuna
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Wahoo
Silky shark
Blacktip shark
Requiem sharks
Common dolphinfish
Rainbow runner
Indo-Pacific sailfish
Marlins
Almaco jack
Hammerhead sharks
Spotted dolphin
Yellowfin tuna
YFT
Predicted consumption of yellowfin tuna
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Wahoo
Silky shark
Requiem sharks
Common dolphinfish
Dolphinfishes
Rainbow runner
Marlins
Almaco jack
Hammerhead sharks
Yellowfin tuna

Fig. 2

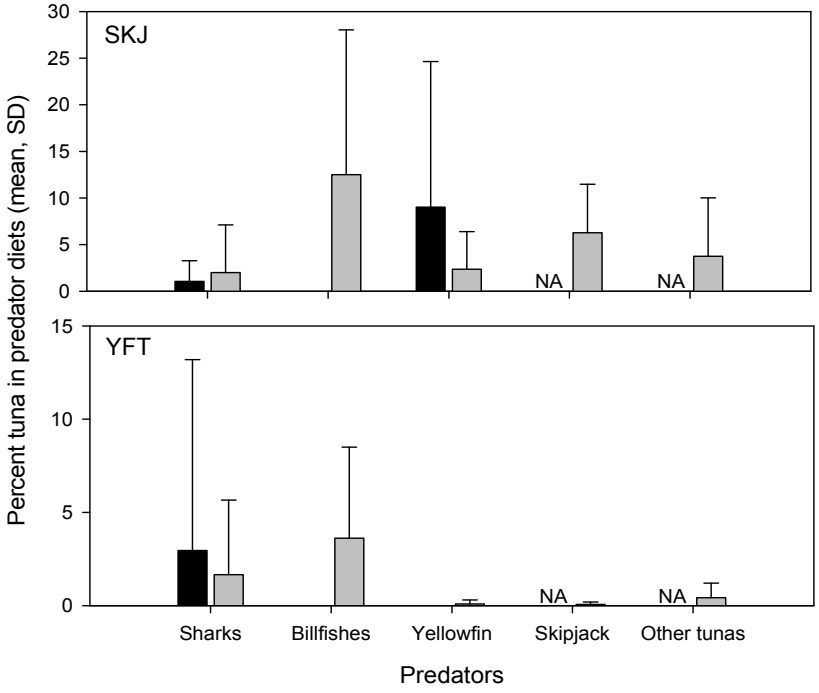
SKJ
YFT
Percent tuna in predator diets (mean, SD)
30
25
20
15
10
5
0
15
10
5
0
NA
NA
NA
NA
Sharks
Billfishes
Yellowfin
Skipjack
Other tunas
Predators

Fig. 3

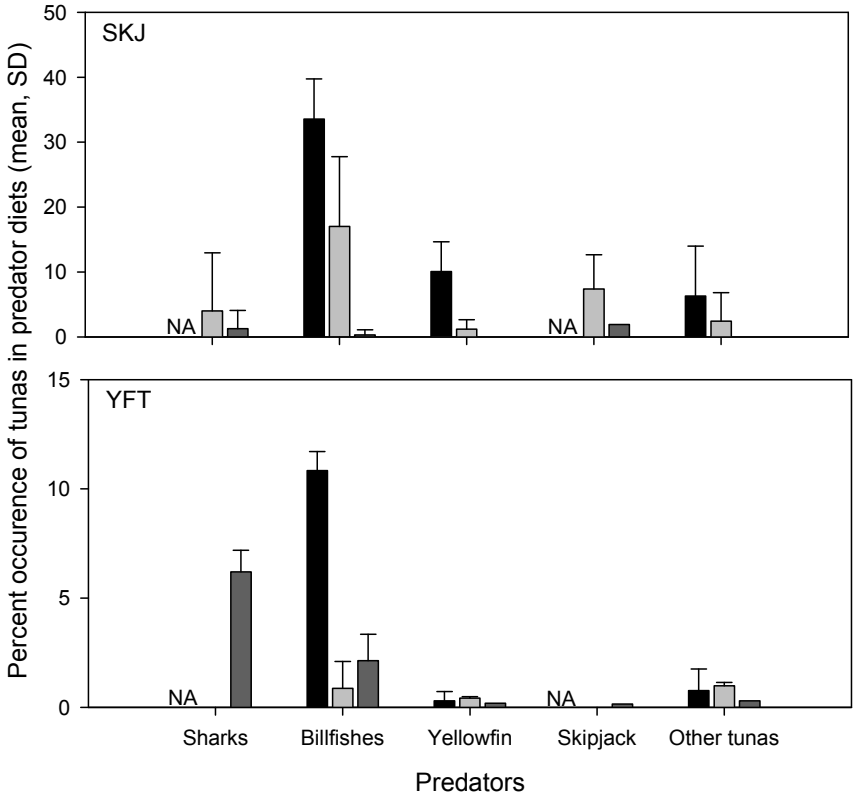
SKJ
YFT
NA
NA
NA
NA
Percent occurence of tunas in predator diets (mean, SD)
Sharks
Billfishes
Yellowfin
Skipjack
Other tunas
Predators

Fig. 4

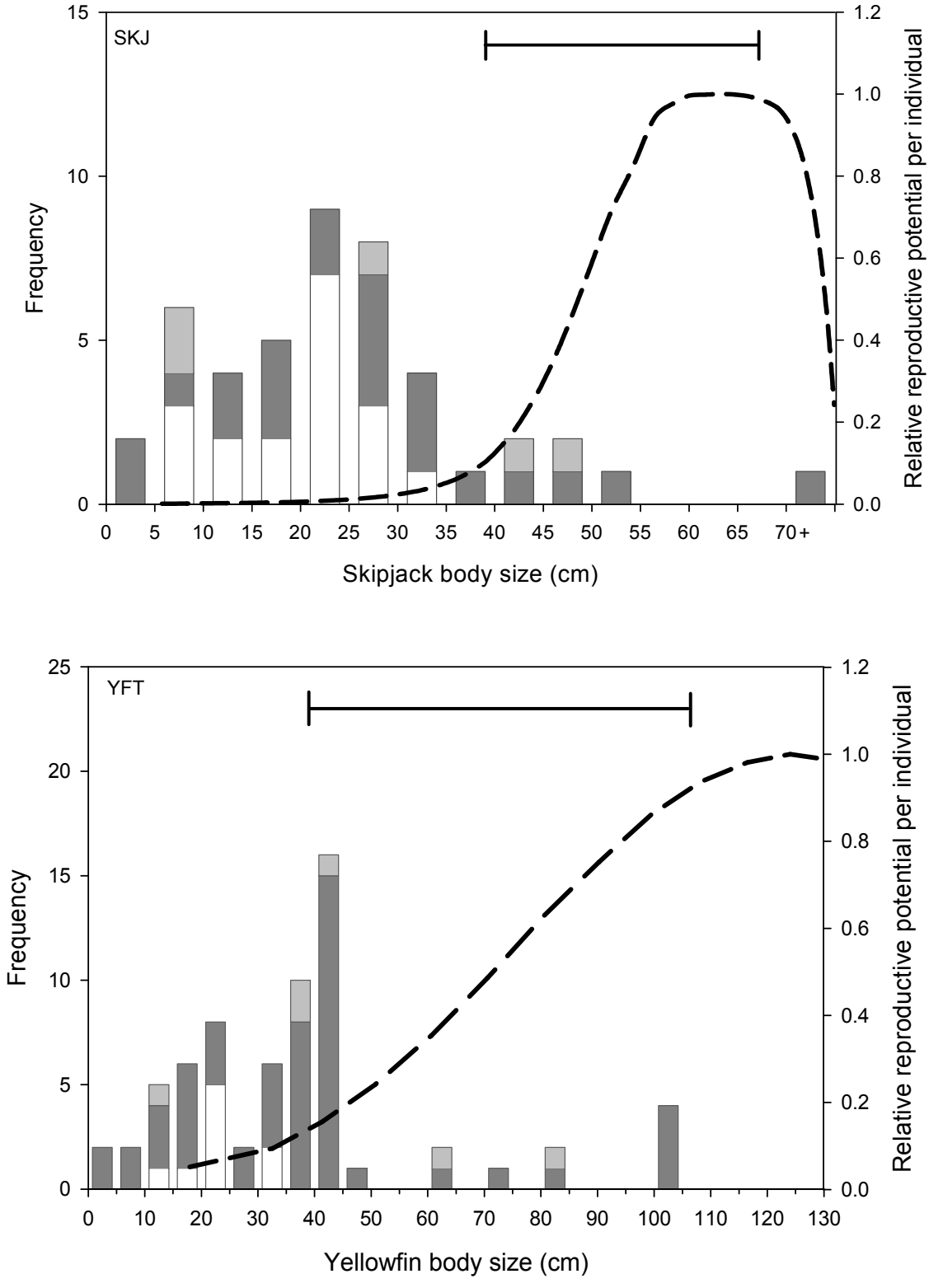
SKJ
Frequency
Relative reproductive potential per individual
Skipjack body size (cm)
0
5
10
15
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70+
YFT
Frequency
Relative reproductive potential per individual
Yellowfin body size (cm)
0
5
10
15
20
25
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0 10 20 30 40 50 60 70 80 90 100 110 120 130

Fig. 5